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PATTERNS OF ACTIVITY OF SUBARCTIC VOLES

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Patterns of Activity of Subarctic Voles" submitted by Thomas Bruce Herman in partial fulfilment of the requirements for the degree of Master of Science.

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Date 17 Feb/75

ABSTRACT

Activity and movements of female red-backed voles, *Clethrionomys gapperi*, were monitored with a radio telemetry system over a 14-month period in a 900 m^2 natural enclosure. Animals exhibited a short-term (2-5 hr.) activity rhythm which remained relatively constant throughout the year and a circadian rhythm which shifted from diurnal in winter to nocturnal and crepuscular in summer. Among anestrous voles, movements and extra-nest activity were minimized during early winter when the subnivean space had not yet developed, and were maximized in late winter-early spring during snowmelt. In summer, activity and movements increased with the progression of reproductive phases from anestrous to lactating. In the face of environmental and physiological fluctuations, animals adjusted their adaptive strategies by altering their patterns of activity.

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INTRODUCTION

Energy budgets and their relation to survival strategies are important components of the ecology of an animal. Although calculation of the absolute energetics of free-ranging individuals is now possible (Gessaman, 1973), such information is of limited value unless the time spent by those animals in various states of activity can be accurately partitioned. While the study of absolute energetics provides an ultimate approach to this problem, the study of energy allocation provides a necessary proximal approach.

There is an appreciable lack of information on the activity of small mammals under natural conditions, and particularly beneath an undisturbed snow cover. Although numerous studies of activity exist, they have been primarily confined to work in highly artificial, or at best semi-natural, enclosures. Despite the importance of these studies it is necessary to recognize that animals may perform differently in the laboratory than in the field (Hart, 1964; Gorecki, 1966).

Until recently, techniques for remote sensing of small mammals have been either limited in scope (Miller, 1957; Buckner, 1964; Bider, 1968), inappropriate for use in natural conditions (Stebbins, 1971, 1972, 1974; Friesen, 1972), or have caused some disturbance to the animal's habitat (Karulin, 1970; Karulin *et al.*, 1973). My study was designed to measure seasonal changes in activity patterns and movements of free-living red-backed voles (*Clethrionomys gapperi*) under natural conditions in the course of a year. Recent developments in monitoring free-living activity of small rodents by radio telemetry

(Chute *et al.*, in press) enabled me to identify underlying activity rhythms, to quantify the amounts of time allocated to different activity states, to locate the positions of animals, and to approximate distances travelled by those animals.

The study was carried out between July 1973 and August 1974, and is part of an ongoing study of the population ecology of *Clethrionomys gapperi* at Heart Lake Biological Station, Northwest Territories (60°51'N., 116°38'W.).

Information regarding population dynamics and winter ecology (Fuller, 1969; Fuller *et al.*, 1969), food habits (Dyke, 1971), circadian rhythms (Stebbins, 1972, 1974) and activity (Friesen, 1972) in semi-natural enclosures is already available from this area.

Problems of energy allocation may be especially critical for small homeotherms inhabiting this region, which is characterized by an extreme environment with strong seasonal fluctuations. Because of their limited capacity to maintain energy reserves and their annual changes in physiological conditions (Sealander, 1972) small homeotherms would be expected to alter their activity patterns and adaptive strategies in the face of environmental fluctuations. In the subarctic there are two major seasons, summer and winter, with sharply contrasting conditions; however, within-season variation is not extreme, especially in the micro-environments inhabited by small mammals (Pruitt, 1957). Autumn and spring are reduced to brief periods of rapid change, both in external conditions and internal physiology, and hence are potentially stressful for small homeotherms (Fuller, 1967; Fuller *et al.*, 1969).

METHODS

Enclosure and Radio Telemetry System

Activity was monitored in a 0.09 ha (0.25 acre) enclosure in undisturbed jack pine (*Pinus banksiana*) forest. Above the enclosure, at a height of 1 m, was an orthogonal grid of antenna wires spaced 1.5 m apart. Individual grid wires were connected by coaxial cables to a central receiving station where an RF receiver could be switched to any given grid wire. An animal, with a transmitter strapped around its neck, was located within 75 cm of the intersection of the two orthogonal grid wires with the strongest relative signal strengths. When signal strengths were strong and consistent it was possible to locate the experimental vole more accurately by interpolating its position between two wires. In addition to locating the animal, the system allowed recognition of three activity states, according to the behavior of the signal. As used, the system demanded manual monitoring, which placed certain restrictions on the design of the sampling regime. Further technical details of the system are given by Chute *et al.* (in press).

Handling of Animals

Experimental animals were obtained by live-trapping in the vicinity of the research station and were held in captivity for various lengths of time. Cages were large (46x36x21 cm), equipped with activity wheels, contained food in excess of requirements, and were kept in temperatures and light conditions approximating those of the natural environment. Summer home ranges of voles at Heart Lake

were known to be larger than the area of the enclosure (A. Bodner, pers. comm.). The discrepancy was less for females (home ranges = 0.3 ha) than for males (home ranges up to 3.0 ha); therefore only females were used in this study. Additional evidence on *C. gapperi* (Beer, 1961) and on *C. glareolus* (Il'jenko and Zubchaninova, 1963) showed a marked decrease in the size of the home range from summer and fall to winter. However, the entire area within the enclosure may not be appropriate for habitation, and evidence from the present study showed frequent travel by voles along the base of the wall during summer. Therefore, for most of the year, the wall provided a potential barrier to movement and on some occasions it may have acted as a real barrier.

Age determination of voles was difficult outside of the breeding season. Only one experimental animal used during fall and winter was definitely an adult. All others used during that time were captured in fall and winter and could have been either adult or immature. During the breeding season (summer) only adults were used.

Only one animal at a time was monitored; therefore during most experimental runs the vole was effectively isolated from other voles. However, deep snow in mid- and late winter prevented the pen wall from acting as a barrier to movement, and some wild voles are known to have entered the pen.

One week before release into the pen a subject was anesthetized with ether and fitted with an inactive transmitter. Immediately before release the transmitter was activated by soldering the battery connection; the animal was weighed, its reproductive condition was noted, and it was released into the enclosure along the base of the

wall. Lactating voles were released with their litters in small nest boxes placed inside chimneys (Pruitt, 1959) located at intervals along the wall. During periods of snow cover all voles were released into the subnivean space via these chimneys. Monitoring of activity began after a 24 hr. familiarization period.

Sampling Regime

Subjects were monitored for two successive 24 hr. periods whenever possible. Within each 0.5 hr. of an experimental run animals were continuously tracked for a 10 min. period which began at a randomly chosen time within the first 20 min. of the 0.5 hr. During this period a position fix was taken every 15 sec. Thus during a 24 hr. run, 1968 fixes were obtained, and for each fix one of three activity states (outside burrow, active inside burrow, immobile inside burrow) was recorded.

Environmental parameters, including light, ambient air temperature, precipitation, and wind, were monitored simultaneously with activity. During periods of snow cover, snow was sampled by layer for depth, denisty, hardness, and crystal size, and subnivean temperatures were recorded.

After completion of each experimental run, voles were recaptured in live-traps placed along the inside base of the walls. In order to minimize disturbance to the habitat, the pen was rarely entered by the investigator.

My initial intention was to obtain data representing as many different seasons and reproductive conditions from each individual as possible. However, this objective was restricted somewhat by predation, mortality in captivity, and a shortage of radios at certain times of the

year. Seasonal allocation of experimental runs was also restricted by a shortage of experimental animals, especially during fall and winter. Therefore greatest emphasis was placed on the potentially critical periods during late fall/early winter and late winter/early spring. During summer animals and radio collars were plentiful and an attempt was made to represent the entire season and all reproductive conditions as equally as possible in the experimental runs.

Immediately after pen construction had been completed, a map showing potential shelters and travel routes was compiled. Particular attention was paid to upturned stumps, rocky areas and fallen trees. When research was completed, surface details of those areas within the pen that had been used as burrow sites and temporary shelters were described as fully as possible. Burrow sites were not excavated in order to minimize habitat disturbance for future research.

RESULTS

Data were obtained for 40 complete 24 hr. experimental runs. General data from these runs have been grouped according to season and reproductive condition of the animals (Table 1). Reproductively active animals occurred only during the summer season, therefore experimental runs during other seasons involved anestrous animals only. Fourteen individuals were represented in the 40 runs, of which three were tested in more than one season and three were tested in more than one reproductive condition.

Despite restrictions placed upon the sampling regime, results suggest that the chosen regime was suitable for determining the

TABLE 1.

SYNOPSIS OF EXPERIMENTAL RUNS PERFORMED BETWEEN JULY 1973 AND AUGUST 1974, ARRANGED BY SEASON AND REPRODUCTIVE CONDITION

SEASON	REPROD. COND.(1)	NO. INDIV-IDUALS	NO. RUNS/ INDIVIDUAL	Σ NO. RUNS	$T_{AMBIENT}$ $\bar{X}$ MAX °C $\bar{X}$ MIN °C	$T_{SUBNIVEAN}$ $\bar{X}$ MAX °C $\bar{X}$ MIN °C	REMARKS
SUMMER (26 May-5 Aug.)	A	3	2,1,2	5	+19.0 + 9.4	— —	
(30 May-26 Aug.)	E	2	2,3	5	+17.3 + 5.7	— —	
(3 July-30 Aug.)	P	4	2,2,2,2	8	+23.0 +12.7	— —	
(29 June-29 July)	L	3	1,2,4	7	+23.6 +12.4	— —	
AUTUMN (25 Sept.-30 Oct.)	A	3	2,2,2	6	+ 7.5 - 0.8	— —	No Snow Cover
EARLY WINTER (13-14 Nov.)	A	1	1	1	- 7.8 -16.7	-4.4 -6.7	Snow Depth: 12.5 cm No Subnivean Space Developed
MID-WINTER (3-5 March)	A	1	2	2	-13.6 -25.8	-6.1 -6.7	Snow Depth: 57.0 cm Subnivean Space Well Developed
LATE WINTER (13-30 April)	A	1	4	4	+ 4.1 - 5.0	+0.8 -2.8	Snow Depth: 53 cm Decreasing to 10-25 cm; Toward End of Period S-N Space Collapsing, Heavy Crust at Night, Snow Free Areas Around Tree Bases, Some Standing Water During Day.
SPRING (8-10 May)	A	1	2	2	+ 5.8 + 1.9	— —	Snowmelt Prominent; No New Vegetative Growth; Snow Patches Still Present.

(1) A - anestrous; E - estrous; P - pregnant; L - lactating

Dates refer to initial and terminal experimental runs appropriate to each category

frequency and duration of the animals' activity periods. An activity period was defined as a duration of activity within or outside the home burrow that was both preceded and succeeded by a 10 min. sampling period of immobility within the home burrow. Only .027 of the activity periods recorded were confined within a single 10 min. sampling period (Figure 1). The majority (.754) extended beyond the limits of one sampling period but included less than four. At the same time, individual sampling periods were of sufficient length to provide relatively large blocks of continual information on movements outside the home burrow.

The choice of a 24 hr. familiarization period prior to initiation of tracking proved generally acceptable for the present study. Distances travelled, time spent outside the home burrow, and an index of exploration (distance run divided by duration of activity outside home burrow) were examined in 13 pairs of contiguous 24 hr. runs. After fulfilling the requirement for equality of variance, the three parameters were tested by paired t-tests (Sokal and Rohlf, 1969) for differences between days 1 and 2. Since none of the parameters showed significant differences ($P \simeq .34, .30, .22$ respectively), it was assumed that the animals were behaving in similar fashions for two successive 24 hr. periods. Although inconclusive this suggests that the voles were familiarized before their experimental runs began.

Activity and Movements

Movements and activity were considered both within and among experimental runs. Special attention was paid to the time spent active within and outside the resident burrow, and inside temporary shelters. Approximate distances travelled and an index of exploration (see above) were

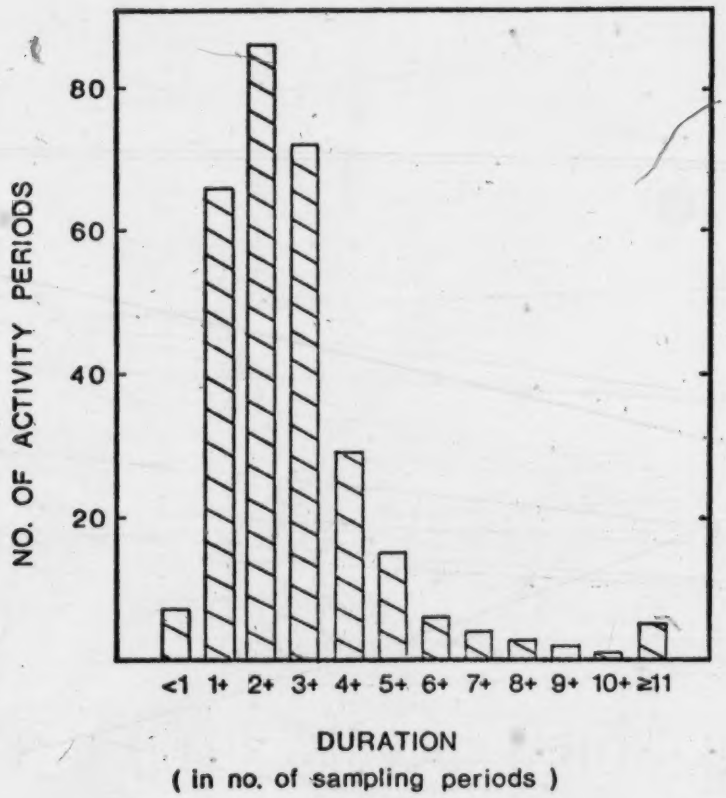

Figure 1. Duration of individual activity periods (time active inside and outside home burrows) expressed as the number of successive 0.5 hr. sampling periods confining a single activity period; based on 296 activity periods from 40 24-hr. experimental runs.

also examined.

Data concerning movements and activity are summarized among runs in Tables 3 and 4 and Figures 2 and 3. A comparison of diurnal and nocturnal activity within runs is presented in Table 2. Diurnal (D) and nocturnal (N) values refer to the periods between sunrise and sunset, and sunset and sunrise, respectively.

Statistical techniques

Data among runs were tested by two-level, mixed-model, nested analysis of variance (Sokal and Rohlf, 1969) for anestrous individuals according to season (Table 3) and for summer individuals according to reproductive condition (Table 4). This test assumes that variances of the error terms of the groups are equal and that the error terms are distributed normally. The validity of these assumptions was tested by an F-max test and a Kolmogorov-Smirnov test for goodness of fit respectively, and was found to hold true for the present data. Since the higher level of classification in these anovas was Model I (i.e. fixed treatment rather than random effects) the analyses were completed with multiple comparisons among means using Duncan's multiple range tests (Steel and Torrie, 1960) for those data showing significant variation among groups ($P < .05$). These were carried out in order to identify the values responsible for the heterogeneity within the anovas.

Data within individual runs were analyzed for differences between diurnal and nocturnal components of activity. The data were then grouped and analyzed by season and reproductive condition. Differences between day and night are summarized in Table 2. Activity outside home burrows was tested individually with 2x2 Chi-squares and was

TABLE 2.

SUMMARY OF DIURNAL (D) VS. NOCTURNAL (N) ACTIVITY FOR ANESTROUS INDIVIDUALS BY SEASON AND FOR SUMMER INDIVIDUALS BY REPRODUCTIVE CONDITION

SEASON	REPROD. COND. (1)	NO. RUNS	ACTIVITY OUTSIDE HOME BURROW		USE OF TEMPORARY SHELTERS		DURATION OF ACTIVITY INCL. INSIDE HOME BURROW		DISTANCE TRAVELLED
			P	H	P	H	P	H	
SUMMER	A	5	D<N (.005)	.005	D>N (.005)	.005	D<N (.005)	.005	D<N (.005)
	E	5	D<N (.005)	.005	D>N (.005)	.005	NS	.005	D<N (.005)
	P	8	D<N (.005)	.005	D>N (.005)	.005	D<N (.05)	NS	D<N (.005)
	L	7	D<N (.005)	.005	D>N (.005)	.005	NS	NS	D<N (.005)
AUTUMN	A	6	D<N (.005)	.005	D<N (.05)	.005	NS	NS	D<N (.005)
EARLY WINTER	A	1	NS	—	NS	—	NS	—	NS
MID-WINTER	A	2	D>N (.005)	.005	D>N (.005)	.005	NS	NS	NS
LATE WINTER	A	4	D<N (.005)	.005	D>N (.005)	.005	D>N (.03)	NS	D<N (.01)
SPRING	A	2	D<N (.005)	—	D>N (.005)	—	D<N (.005)	NS	D<N (.01)

(1) A - anestrous; E - estrous; P - pregnant; L - lactating

See Tables 3 and 4 for group means. See text for details of statistical analysis. P represents significance level of difference between D and N; H represents significance level of heterogeneity among individual runs within groups.

TABLE 3.

SUMMARY OF NESTED ANALYSIS OF VARIANCE DATA (BY DAY, NIGHT, AND 24 HOURS) FOR ANESTROUS INDIVIDUALS ACCORDING TO SEASON

		MEANS						AMONG GROUPS				AMONG INDIVIDUALS WITHIN GROUPS				WITHIN INDIVIDUALS (ERROR)			MULTIPLE COMPARISONS AMONG MEANS (AT .05 SIGNIF. LEVEL)
		SUMMER	AUTUMN	EARLY WINTER	MID-WINTER	LATE WINTER	SPRING	df	SS	MS	P	df	SS	MS	P	df	SS	MS	
Activ. Outside Home Burrow No. Fixes	D	72.4	56.5	41.0	148.0	174.8	24.0	5	54842.	10968.	.022*	4	50464.	12616.	.017*	10	24740.	2474.	SP EW A SU MW LW
	N	200.8	238.8	70.0	118.5	223.3	237.5	5	43583.	8717.	.456	4	43853.	10963.	.341	10	85585.	8558.	
	24	273.2	295.3	111.0	266.5	398.0	261.5	5	82539.	16508.	.237	4	136087.	34022.	.054	10	100674.	10087.	
Use of Temp. Shelters No. Fixes	D	34.8	13.5	28.0	56.0	59.3	12.5	5	6977.	1395.	.258	4	12585.	3146.	.049*	10	8966.	896.6	
	N	8.8	49.8	40.0	10.0	36.7	9.0	5	6520.	1304.	.003***	4	4843.	1211.	.006**	10	1694.	169.4	SU SP MW LW EW A
	24	43.6	63.3	68.0	66.0	96.0	21.5	5	96647.	1933.	.144	4	20555.	5139.	.012*	10	9067.	906.7	
Activ. Outside - Temp. Sh. Use No. Fixes	D	37.6	43.0	13.0	92.0	115.5	11.5	5	25266.	5053.	.013*	4	14637.	3659.	.039*	10	9608.	960.8	SP EW SU A MW LW
	N	192.0	189.0	30.0	108.5	186.5	228.5	5	38647.	7729.	.408	4	35978.	8995.	.332	10	68842.	6884.	
	24	229.6	232.0	43.0	200.5	302.0	240.0	5	57411.	11482.	.286	4	69741.	17435.	.141	10	78797.	7880.	
Approx. Dist. Travelled Meters	D	58.4	58.4	11.1	136.8	159.4	48.9	5	45297.	8659.	.176	4	38960.	9740.	.146	10	44892.	4489.	
	N	758.9	432.8	91.8	84.8	850.1(1)	501.2	5	1215140.	243028.	.430	4	527462.	131866.	.679	9	2015976.	223997.	
	24	817.3	491.2	102.9	221.6	963.7(1)	550.1	5	1241036.	248207.	.350	4	560539.	140135.	.597	9	1740670.	193408.	
Index of Exploration	D	57.9	27.0	11.1	26.4	27.5	16.3	5	4568.	913.5	.079	4	36103.	9026.	.000***	10	3279.	327.9	
	N	130.0	58.7	30.6	18.9	117.4(1)	84.9	5	29116.	5823.	.104	4	10910.	2728.	.374	9	20425.	2269.	
	24	116.5	52.1	25.7	24.2	89.5(1)	73.5	5	19888.	3978.	.135	4	12382.	3096.	.219	9	15761.	1751.	
X Dur. Act. Pd Out & In Bur Minutes	D	56.9	80.8	60.0	75.0	60.3	58.0	5	2177.	435.4	.494	4	1716.	429.0	.485	10	4617.	461.7	
	N	183.0	71.2	51.4	70.0	93.8	375.0	5	173315.	34663.	.000***	4	33911.	8478.	.004***	10	10597.	1060.	EW MW A LW SU SP
	24	78.8	75.8	52.5	71.1	72.7	107.5	5	2626.	525.3	.070	4	1419.	354.7	.175	10	1797.	179.7	
X PERIOD ACTIVITY PEAKS (24) MINUTES		228.0	182.0	180.0	223.0	201.8	223.0	5	7776.	1555.	.132	4	1612.	403.0	.686	10	6989.	698.9	

(1) Includes incomplete data because of activity beyond confines of pen during one experimental run. Figures are therefore conservative.

Day and night values are absolute, and remain unadjusted for seasonal changes in relative day/night lengths. Distances travelled are adjusted (X3) to cover entire 24-hr. period. SS= sum of squares; MS= mean square; P= probability of the sample variance ratio. *, **, and *** represent significance at .05, .01, and .005 levels respectively. In multiple comparisons among means, those sets of means (seasons) underlined are not significantly (.05) heterogeneous.

TABLE 4.

SUMMARY OF NESTED ANALYSIS OF VARIANCE DATA (BY DAY, NIGHT, AND 24 HOURS) FOR SUMMER INDIVIDUALS ACCORDING TO REPRODUCTIVE CONDITION

		GROUP MEANS				SOURCE OF VARIATION										MULTIPLE COMPARISONS AMONG MEANS (At .05 Level)
						AMONG GROUPS				AMONG INDIVIDUALS WITHIN GROUPS				WITHIN INDIVIDUALS (ERROR)			
		ANESTROUS	ESTROUS	PREGNANT	LACTATING	df	SS	MS	P	df	SS	MS	P	df	SS	MS	
Activity Outside Home Bur. No. Fixes	D	72.4	198.0	182.6	324.1	3	191454.	63818.	.001***	8	72618.	9077.	.286	13	84775.	6521.	A P E L
	N	200.8	213.6	202.9	145.6	3	18460.	6153.	.195	8	57841.	7230.	.109	13	44188.	3399.	
	24	273.2	411.6	385.5	469.7	3	115104.	38368.	.053	8	152104.	19013.	.203	13	149750.	11519.	
Use of Temporary Shelters No. Fixes	D	34.8	87.4	58.9	54.4	3	7102.	2367.	.054	8	45843.	5730.	.001***	13	9315.	716.6	
	N	8.8	32.0	17.9	9.6	3	1849.	616.3	.111	8	1859.	232.4	.531	13	3288.	253.0	
	24	43.6	119.4	76.8	64.0	3	15658.	5219.	.009**	8	51940.	6493.	.001***	13	11363.	874.1	A L P E
Act. Out. - Temp. Shelt. Use No. Fixes	D	37.6	110.6	123.7	269.7	3	176077.	58692.	.0004***	8	45426.	5678.	.352	13	59706.	4593.	A E P L
	N	192.0	181.6	185.0	136.0	3	12885.	4295.	.331	8	63174.	7897.	.088	13	44594.	3430.	
	24	229.6	292.2	308.7	405.7	3	96907.	32302.	.051	8	119213.	14902.	.228	13	124114.	9547.	
Approx. Distance Travelled Meters	D	58.4	168.1	228.8	617.9	3	1125165.	375055.	.0001***	8	138159.	17270.	.579	13	264631.	20356.	A E P L
	N	758.9	518.0	771.6	508.2	3	404661.	134887.	.407	8	2014257.	251782.	.138	13	1684868.	129605.	
	24	817.3	686.1	1000.4	1126.1	3	668800.	222933.	.276	8	1691360.	211420.	.296	13	4370560.	154646.	
Index of Exploration	D	19.0	27.5	38.3	60.0	3	5752.	1917.	.011**	8	2424.	303.0	.551	13	4428.	340.6	A E P L
	N	130.4	77.7	120.0	128.9	3	9612.	3204.	.190	8	28724.	3590.	.119	13	22692.	1746.	
	24	116.5	52.5	85.8	78.5	3	10447.	3482.	.076	8	20831.	2604.	.105	13	15673.	1206.	
$\bar{X}$ Dur. Act. Per. Out. & In. Bur. Minutes	D	56.9	67.1	75.7	121.3	3	15373.	5124.	.008**	8	5160.	645.0	.629	13	10768.	828.3	A E P L
	N	183.0	120.0	102.8	130.7	3	20489.	6830.	.242	8	70418.	8802.	.123	13	56257.	4327.	
	24	78.8	74.9	85.1	120.3	3	8310.	2770.	.043*	8	4998.	624.8	.602	13	9954.	765.7	E A P L
$\bar{X}$ PERIOD ACTIVITY PEAKS (24) MINUTES		225.0	187.6	205.5	185.9	3	6310.	2103.	.154	8	9043.	1130.	.415	13	13212.	1016.	

Distances travelled are adjusted (X3) to cover entire 24-hr. period. SS= sum of squares; MS= mean square; P= probability of the sample variance ratio. *, **, and III represent significance at .05, .01, and .005 levels respectively. In multiple comparisons among means, those sets of means (reproductive phases) underlined are not significantly (.05) heterogeneous.

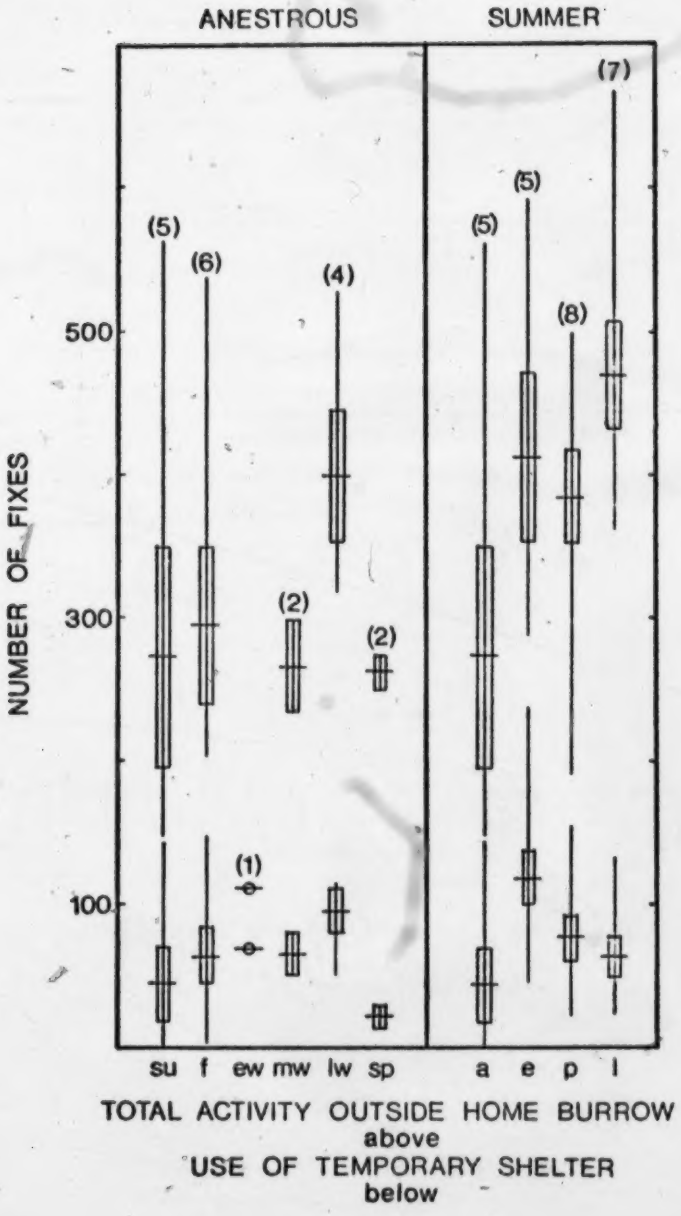

Figure 2: 24-hr. activity outside home burrow and use of temporary shelters for anestrous voles according to season and summer voles according to reproductive condition; mean ± std. error, and range. Sample size in parentheses above each group. su= summer, f= fall, ew, mw, lw= early, mid-, and late winter, sp= spring; a= anestrous, e= estrous, p= pregnant, l= lactating.

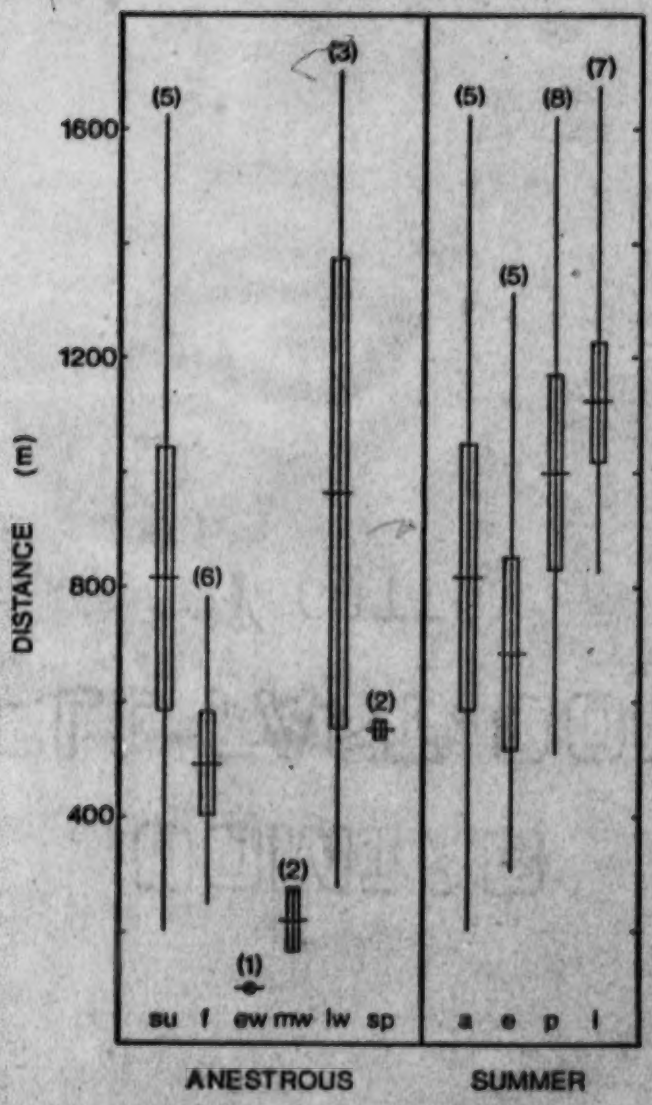

Figure 3. Distances travelled per experimental run by anestrous voles according to season and summer voles according to reproductive condition. Distances are adjusted (X3) to cover entire 24-hr. period; mean ± std. error, and range. Sample size in parentheses above each group. su= summer, f= fall, ew, mw, lw= early, mid-, and late winter; a= anestrous, e= estrous, p= pregnant, l= lactating.

tested by groups with a Chi-square test for heterogeneity (Sokal and Rohlf, 1969). These tests compared diurnal and nocturnal activity weighted according to the relative lengths of day and night, and should provide a more accurate measurement of diurnal or nocturnal preferences than tests which only compare absolute values, regardless of light regime. Diurnal and nocturnal use of temporary shelters weighted according to the total amount of time spent outside home burrows during day and night was tested similarly. Any activity components within runs that exhibited an expected frequency of 5 or less were excluded from these analyses. Durations of diurnal and nocturnal activity periods were compared by nested analysis of variance, after meeting the necessary criteria for the test, including equality of variance and normality (see above). Distances travelled were weighted according to the number of sampling periods spent outside the home burrow, and were tested in individual runs by unpaired t-tests of the differences between diurnal and nocturnal means. They were then tested among groups by combining probabilities from the independent unpaired t-tests (Sokal and Rohlf, 1969).

Diurnal vs. nocturnal

During summer, all four reproductive groups exhibited significantly less activity ($P < .005$) outside of home burrows during the day than at night, both in amount of time spent and distance travelled (Table 2). They also showed significantly greater diurnal than nocturnal use of temporary shelters ($P < .005$). Anestrous and pregnant animals were active inside and outside the home burrow for shorter periods during the day than at night ($P < .005$, $< .05$ respectively), while estrous and

lactating individuals showed no significant differences.

Anestrous voles spent more time outside the home burrow ($P < .005$) and travelled greater distances ($P < .01$) at night than in the day during summer, autumn, late winter, and spring. In mid-winter there was greater diurnal than nocturnal activity ($P < .005$), although there were no significant differences in distances travelled. Temporary shelters were used more in the day than at night during summer ($P < .005$), mid- and late winter, and spring, while animals in autumn used temporary shelters more at night ($P < .05$). The duration of diurnal activity periods was shorter than nocturnal ones during summer, late winter, and spring ($P < .005$, $< .05$, $< .005$ respectively), but did not differ significantly during autumn and early and mid-winter. The single early winter run exhibited no significant day/night differences in activity or movements.

Seasonal comparisons

A comparison of movements and activity in anestrous individuals among different seasons is provided in Table 3 and Figures 2 and 3. There are many apparent differences but few are significant. On a 24 hr. basis the amount of activity outside the home burrow appeared constant in most seasons, excluding a possible decrease in early winter and increase in late winter. Distances travelled apparently decreased from summer to early and mid-winter and rebounded in late winter. The late winter value is an underestimate due to travel beyond the confines of the pen because of deep snow. Activity in mid-winter was limited to subnivean travel, but towards late winter extensive supranivean activity occurred at night. The use of temporary shelters relative to time

spent outside the home burrow apparently increased in autumn and reached a maximum in early winter. It then declined to a minimum in spring.

During the day, when tested by multiple comparisons among means for all seasons, activity outside the burrow was significantly lower in spring than in other seasons, and significantly higher during mid- and late winter when the subnivean space was well developed. Distances travelled appeared greater in mid- and late winter than during the rest of the year but the differences were not significant. The index of exploration was highest in summer and lowest in early winter and spring. Temporary shelters were apparently used less in autumn and spring and more in mid- and late winter, but not significantly so.

During the night, activity outside the burrow and distances travelled were similar in summer, autumn, late winter, and spring, but were apparently less in early and mid-winter. Index of exploration was highest in summer and late winter and lowest in mid-winter. When compared among all seasons, temporary shelters were used significantly less in summer, spring, and mid-winter and significantly more in autumn.

The durations of activity periods during daylight and over a 24 hr. period did not differ significantly, but at night they were significantly longer in spring and summer than during the rest of the year.

Reproductive comparisons

Movements and activity of voles during summer are compared among different reproductive states in Table 4 and Figures 2 and 3. During daylight, anestrous voles were significantly less active outside of the

home burrow than estrous and pregnant ones, which in turn were less active than lactating ones. Anestrous animals were significantly less active than the three remaining groups in terms of duration of overall activity periods, distances travelled, and the index of exploration. In contrast, there were no significant differences at night in any of the parameters measured.

Over a 24 hr. period, anestrous animals appeared less active than those in the other three groups, and estrous individuals tended to use temporary shelters more than any other group. Lactating animals were active for significantly longer periods than all others.

Short-term and circadian rhythms

Although there are some significant differences in the duration of activity periods, on a 24 hr. basis the mean period, and therefore frequency of occurrence of activity peaks, did not differ significantly in either the seasonal or the reproductive group. This strongly suggests that these activity periods represent a relatively constant short-term activity cycle of 2-5 hrs. as described for *C. gapperi* by Priesen (1972). On the other hand, differences between the nocturnal and diurnal intensities of activity during these short-term periods within individual runs (Table 2) are assumed to represent an overlying circadian rhythm, which shifted on an annual basis from intensely nocturnal in summer to weakly diurnal in winter. The timing of activity periods seemed related to sunset and sunrise in summer, fall, and early winter, with a peak normally occurring immediately prior to sunrise and following sunset. Strong correlations between sunset and onset of activity periods, and sunrise and cessation of activity periods during

these seasons are shown in Figure 4. The correlation between sunset and onset of activity was tested with a Chi-square for goodness of fit to a 1:1 ratio by comparing onset during the 0.5 hr. which included sunset and the 1.0 hr. which followed with onset during the subsequent 1.5 hr. A significantly greater ($P < .01$) number of activity periods began in the first 1.5 hr. than in the second. The correlation between sunrise and cessation of activity was tested similarly by comparing cessation during the 1.5 hr. immediately surrounding sunrise with cessation during the preceding 1.5 hr. A significantly greater ($P < .025$) number of activity periods terminated near sunrise than in the preceding 1.5 hr. During mid- and late winter, and spring, there was no apparent correlation of the timing of these periods with light regime (Figure 4), or with any other environmental stimuli.

It is obvious from Tables 2, 3, and 4 that for some parameters there is considerable variation within individuals and among individuals within groups. However, the seasonal changes in circadian rhythms exhibited within individuals tested in more than one season (Table 5) and the lack of individual variation within reproductively active groups for activity parameters that differed among groups (Table 4) suggest that differences among groups generally are due to changes in physiological and environmental conditions rather than to individual variation.

Use of Shelters

Considerable information on the use of burrows and temporary shelters was derived from the study. Although the animals probably altered to some extent the naturally occurring subterranean spaces which they occupied, there was no evidence of extensive digging within

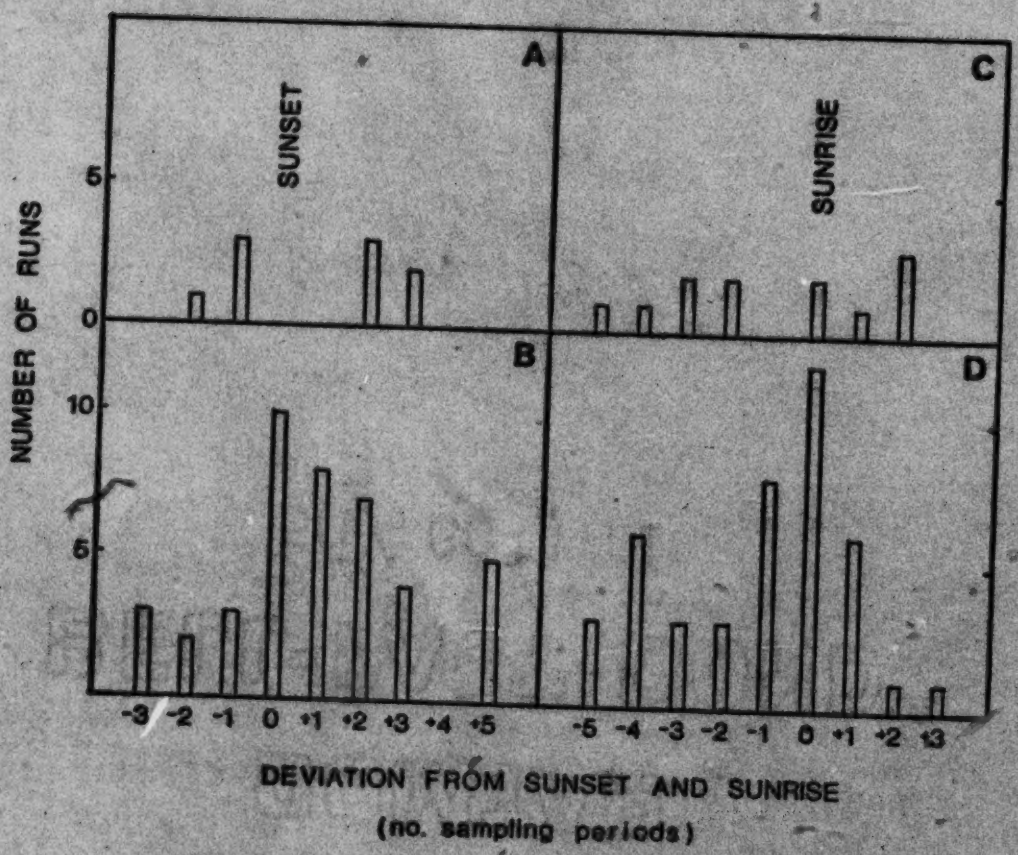

Figure 4. Onset of activity periods in relation to sunset (A,B) and cessation of activity periods in relation to sunrise (C,D) during summer, fall, early winter (B,D) and mid-winter, late winter, spring (A,C). Sampling periods refer to the randomly chosen 10 min. duration, within each 0.5 hr. of a run, in which an activity period commenced (A,B) or ceased (C,D), in relation to the 0.5 hr. in which sunset (A,B) or sunrise (C,D) occurred. Positive values refer to those intervals following sunset and sunrise, and negative values refer to those preceding sunset and sunrise.

TABLE 5.

COMPARISONS OF DIURNAL AND NOCTURNAL ACTIVITY PARAMETERS IN INDIVIDUALS TESTED IN MORE THAN ONE SEASON

SUBJECT	NO. RUNS	DATE OF RUN(S)	DAY/NIGHT DURATION (NO. OF FIXES)	MEAN ACTIVITY OUTSIDE HOME BURROW (NO. OF FIXES)			MEAN USE OF TEMPORARY SHELTERS (NO. OF FIXES)			MEAN DISTANCE TRAVELLED (M)		
				D	N	DIFFERENCE (P)	D	N	DIFFERENCE (P)	D	N	DIFFERENCE (P)
#1	1	23-24 July	1456/512	329	172	D<N (.005)	82	3	D>N (.005)	328.2	366.3	NS
	1	13-14 Nov.	610/1358	41	70	NS	28	40	NS	11.1	91.8	NS
#7	2	28-30 Oct.	730/1238	52	324	D<N (.005)	25	85	D<N (.005)	6.9	41.8	D<N (.01)
	2	3-5 Mar.	873/1096	148	118	D>N (.005)	56	10	D>N (.005)	26.4	18.9	NS
#11	2	8-10 May	1378/500	24	237	D<N (.005)	12	9	—	48.9	501.2	D<N (.01)
	2	26-28 May	1501/467	20	228	D<N (.005)	1	0	—	32.4	1133.8	D<N (.01)

Taken from the analysis of diurnal vs. nocturnal activity within runs. See text for details.
#1 tested in summer and early winter; #7 in fall and mid-winter; #11 in spring and summer.
P represents significance level of difference between D and N.

the enclosure. Thirteen different spaces were utilized for sleeping or for temporary shelter during the 40 experimental runs. All were used as temporary shelters and eleven as home burrows. If a vole spent a period of immobility (presumably sleep) between two distinct peaks of activity in any subterranean space, that space was considered a home burrow. If a space was not slept in but was used for other purposes it was considered a temporary shelter. Eight shelters were located within or beneath the bases of decaying windthrown trees and contained multiple (2-5) small entrances 2.5-3.5 cm. in diameter. Three, also with multiple entrances, were located in rock outcrops with overlying vegetative cover; and one relatively open shelter was situated in an outcrop beneath several small windthrown trees. The shelter most frequently utilized as a home burrow (by 7 individuals, in 17 out of 40 experimental runs) was located beneath a mound of soil 10 cm. high and 45 cm. in diameter at the base of a live twin-trunked jack pine (*P. banksiana*). It contained three small entrances around the perimeter of the mound, was covered with pine needles, and was sheltered from above by an extensive cover of juniper (*Juniperus communis*) and buffaloberry (*Shepherdia canadensis*).

During late winter one vole built an above-ground nest at the base of one of the trapping chimneys. It was constructed of terylene which had been used to insulate live traps for removal of animals from the pen, and was used in two successive 24 hr. experimental runs.

Seasonal preferences and burrow sharing

The home burrow most frequently used during spring and summer (in 16 of 27 runs) was occupied only once during fall and never during

winter, and was used by several pregnant and lactating individuals in quick succession. The home burrow used most frequently in autumn was utilized in all six runs but was used in only two runs during the remainder of the year. During mid- and late winter one subterranean home burrow and one above-ground nest were used exclusively in the six runs and were not utilized for home burrows at any other time of year. On the other hand, one temporary shelter was used in only one season, five in two seasons, four in three seasons, and three in four seasons. Therefore there appeared to be greater seasonal preferences for home burrows than for temporary shelters.

Pregnant and lactating animals and early and mid-winter anestrous animals tended to use only one home burrow per run. The average for estrous animals was 1.4 home burrows per run and for autumn animals was 2.0.

There was strong evidence during mid- and late winter from tracks and from livetrapping in the vicinity of burrows that experimental voles were sharing their burrow complexes with wild voles (both male and female) and deer mice (*Peromyscus maniculatus*). Deer mice could enter the pen in any season, but voles could only cross the wall during periods of deep snow cover.

Food storage

The number of re-entries into home burrows was examined in relation to the number of activity periods spent outside home burrows as an indirect indicator of whether or not animals were storing food. It was assumed that the greater the number of re-entries, the greater the

probability that voles were engaged in food storage. Individuals were first tested by a Chi-square for goodness of fit to a 1:1 ratio, and were then tested together by a Chi-square for heterogeneity (Sokal and Rohlf, 1969). The latter not only gives a more sensitive test for significance (because of increased sample size) but also reflects the amount of variation among runs. The majority of runs (.75) show no significant differences on an individual basis. Excluding one fall and one mid-winter run, all which show a significant difference involved either pregnant or lactating individuals. When considered together the number of burrow re-entries (1.83 per activity period) is significantly greater ($P < .005$) than the number of activity periods, and the Chi-square for heterogeneity is significant ($P < .05$). However, when burrow re-entries known to be due to movements of litters or bedding are removed from the analysis, the Chi-square for heterogeneity is no longer significant. This suggests that individual runs are similar throughout the year. Although the number of re-entries (1.63 per period) is still significantly greater than the number of activity periods, the difference is so small that any extensive storing of food is unlikely.

DISCUSSION

Rhythms

A short term rhythm has been demonstrated in many rodents and its malleability has been attributed to environmental heterogeneity (Ashby, 1971) and food availability (Davis, 1933; Wald and Jackson, 1944; Grodzinski, 1962). In *C. glareolus* (Miller, 1955; Brown, 1956) and

C. gapperi (Friesen, 1972) it has usually been attributed to a feeding cycle, but in the varying lemming (*Dicrostonyx groenlandicus*) (Hansen, 1957) it was shown to be largely endogenous and independent of food. Evidence from the present study suggests that this short term rhythm may have several components. Despite variation within runs, the relative constancy of the short term activity cycle among runs suggests the existence of an endogenous component. This is supported by the occurrence of frequent activity periods in which no activity took place outside of the home burrow. Since voles probably did not store food, this would suggest that they did not feed during every activity period. On the other hand, the increase in duration of short term activity in lactating animals was probably the response of a feeding rhythm to an increased energy demand.

Circadian rhythms overlying the short term rhythms in *C. gapperi* have been discussed by Stebbins (1972, 1974). He also reported marked seasonal changes in these rhythms at Heart Lake, from nocturnal in winter to diurnal, with a crepuscular component, in summer. The rather substantial discrepancy between his results and those of the present study might be accounted for by any of several factors. The relatively homogeneous and spatially limited environments of Stebbins' experimental voles may have affected the animals' activity patterns. Also, the two studies may have measured different parameters, since experimental apparatuses and criteria for identifying rhythms differed substantially between the two.

In a seasonally fluctuating environment it would be of obvious advantage to adjust circadian rhythms accordingly (Bünning, 1964).

Erkinaro (1974) has demonstrated an endogenous circannual inversion of activity in *C. glareolus* and *M. agrestis* from diurnal in winter to nocturnal in summer, each with two recognizable phases. Evidence from Friesen (1972) and from the present study suggests a similar inversion in *C. gapperi*, but seasonal changes in the intensity of the peak as well as in its timing often make it difficult to differentiate major and minor peaks of activity. In summer and fall, both sunrise and sunset appeared important in entraining the short term activity cycle to a circadian rhythm, similar to that reported by Pearson (1962) for *C. glareolus* and *C. rufocanus*. Other workers have demonstrated the importance of light in determining the timing of activity patterns (Erkinaro, 1961; Swade and Pettindrigh, 1967) and of temperature in determining the intensity of those patterns (Sweeney and Hastings, 1960; Gebczynski, 1964).

A seasonal change in intensity could be considered a measure of the relative importance of maintaining circadian patterns at different times of the year. In the present study the switch to a diurnal pattern in winter is accompanied by decreased intensity and more labile timing. This lability suggests that either a zeitgeber (Aschoff, 1960) is lacking or that it is advantageous for the rhythms not to be precisely entrained. The subnivean space is noted for the constancy of its environmental parameters, and although an occasional visit to the surface during the day could alter the phase of the rhythms (Bruce, 1960) it probably could not act as an accurate zeitgeber (Aschoff, 1960).

It is difficult in this case to envision an adaptive advantage to

entraining to an almost constant environment, if it is possible. On the other hand, lack of precise entrainment might decrease the probability of predation and be advantageous.

Use of Shelters

Apparent seasonal changes in preferences for certain burrows can be attributed to any of several factors. There are undoubtedly seasonal changes in the relative accessibility and insulation of different burrows, and it is easy to imagine a situation where one burrow is more appropriate than another for only part of the year. The most extreme example is that of subnivean surface nesting in winter, reported to be prevalent in *C. glareolus* in some cases (Koshkina, 1957) but absent in others (Coulianos and Johnels, 1962). In the discussion of the use of above-ground subnivean nests by voles, Formozov (1946) mentioned the disadvantage of increasing the probability of predation and the advantages of lowering heat exchange from the nest to the environment and lessening the problem of rime formation in the burrow. Evidence for a seasonal change in preference in the present study includes the use of a relatively open subterranean burrow in mid- and late winter as well as construction of an above-ground subnivean nest, albeit with introduced materials.

On the other hand, it is possible that an animal is attracted to a burrow that has been used previously, and the more recently used, the more attractive it may be. Such a mechanism could conceivably be misinterpreted as a seasonal change in preference. Our knowledge of social systems in *C. gapperi* is limited, and chemo-communication in rodents in general is poorly understood. Smirin and Smirin (1974)

showed that *C. glareolus* tends to use burrows separately, but they reported some concurrent use of nests. In the light of Friesen's (1972) observations of intense intraspecific aggression by lactating voles, it is interesting that in the present study the same burrow was used by several pregnant and lactating individuals in quick succession. Moreover, it seems that a strategy of this sort would result in the buildup of ectoparasites and in the fouling of the nest or nest locality with feces.

Despite these problems, concurrent use of nests has a number of advantages at certain times of the year and has been demonstrated in many small rodents, including *C. gapperi* (Friesen, 1972; Stebbins, 1972). Aggregation in late fall and early winter allows animals to use only the best parts of a mosaic of good and bad habitats (Fuller, 1967) in addition to providing them with a more efficient means of thermoregulation through huddling. Subnivean forms tend to lose weight during winter (Fuller *et al.*, 1969) and hence increase their surface to volume ratio, and huddling would provide them with an effective decrease in surface to volume ratio for a large part of each day.

Both huddling and nest use have been shown to be important in regulating metabolic rates (Howard, 1951; Sealander, 1952), although several workers (Cotton and Griffiths, 1967; Gebczynska and Gebczynski, 1971; Tertil, 1972) have more recently demonstrated that use of an insulated nest is the more important of the two at low temperatures.

The energetic costs of obtaining food may become critical in cold temperatures (Schwarz, 1967; Sadleir *et al.*, 1973) and one would expect a minimum amount of activity outside the nest during periods

of cold stress. This can be accomplished by obtaining food more economically or by decreasing absolute food intake. Miller (1955) reported food storage by *C. glareolus* under conditions of decreasing daylength and Stebbins (1972) found storage of seeds by *C. gapperi* in nest boxes during winter. However, evidence from the present study and from Friesen (1972) suggests that food storage is probably limited in *C. gapperi*. Taking into consideration the food preferences of this species (Dyke, 1971), one might conclude that food storage could become too energy intensive a process to be worthwhile. In the present study, animals apparently economized by utilizing temporary shelters for feeding. In fall and winter a large proportion of the time spent outside the home burrow was spent inside these shelters, especially at night when temperatures were lowest. In addition to providing insulation against unfavorable environmental conditions (cold temperatures in fall and winter, low humidity in summer) the use of such shelters should decrease the incidence of predation. By decreasing extra-nest activity in addition to increasing use of temporary shelters, voles reduced their exposure time to the winter environment without changing the frequency or duration of their overall activity periods.

A decrease in the absolute food intake of *C. gapperi* during winter has been suggested by Dyke (1971). Such a decrease has been noted in other cricetids and has been accomplished by acclimatization of the metabolism to lower temperatures (Pearson, 1962; Gorecki, 1966, 1968), increase in body insulation (Hart, 1956, 1964), increase in nest insulation (Gorecki, 1968), and by elimination of breeding (Gorecki,

1968; Hansson, 1970).

Reproductive Activity

Winter breeding has never been reported for *C. gapperi* in the vicinity of the study area and Fuller (1969) suggested that a persistent snow cover and cold temperatures in spring may even retard the onset of reproduction. Winter breeding in *C. glareolus* has occurred only in association with mild winters (Zejda, 1962) or abundant food resources (Smyth, 1966) and has always been of lesser intensity than summer breeding. Increases in activity of reproductively active animals in the present study suggest that the energetic costs of reproduction in *C. gapperi* are high. Similar increases have been reported for other voles (Kaczmarski, 1966; Migula, 1969). Since it occurs concomitantly with the spring weight gain, the onset of breeding may be especially energy expensive in subnivean mammals (Kalela, 1957; Fuller *et al.*, 1969; Merritt, 1974). In the present study none of the experimental animals became estrous until late May, several weeks after snowmelt, when food was presumably more plentiful due to new vegetative growth (Dyke, 1971), and environmental stress was presumably relaxed due to warmer temperatures and cessation of spring flooding.

Movements

Fuller (1969) stressed the importance of both fall and spring critical periods in influencing overwinter survival and the success of the following breeding season. Therefore it would seem valuable to look at movements during those periods as well as during the time intervening.

Fall movements of cricetids have been described by several workers. Myllymäki *et al.* (1962) observed a nocturnal fall migration in lemmings (*L. lemmus*) which functions as a means of both redistribution and seasonal habitat change. Bodner (pers. comm.) observed a redistribution of *C. gapperi* during fall, and Martell (pers. comm.) and Švarc *et al.* (1964) reported a similar phenomenon in *C. rutilus*, but the extent of these movements is unknown. Koshkina (1957) noted an increase in activity of *C. glareolus* and *C. rutilus* during fall, concomitant with an increasing scarcity of food. Data from the present study showed no change between summer and fall in the amount of time spent active outside the burrow but showed an apparent decrease from summer to fall in the distance travelled. On the other hand the fact that they used a greater number of burrows during fall suggests that these animals may have been less settled than animals at other times of the year. It is possible that the wall affected the movements of subject voles, either directly by providing a barrier, or indirectly by isolating them from other voles whose presence might have provided a stimulus to movement.

During early winter, before stabilization of snow cover, movements of the one animal tracked were limited and activity outside the burrow was greatly reduced. The animal was presumably under thermal stress and its vulnerability to predation was documented by its disappearance during the course of the experimental run.

Data on the extent and types of mid-winter movements of voles (Rotshild, 1956; Smirin, 1970; Karulin, 1973) vary considerably, and strongly suggest that local conditions such as ambient and subnivean temperatures, food availability, and snow conditions play an important role in their determination. Mid-winter runs in the present study

showed no evidence of supranivean travel although ambient air temperature was not extreme, and subnivean movements were relatively short and localized.

Late winter and early spring movements in the pen were the most extensive of any shown by anestrous animals throughout the year. The first and second runs during these periods were carried out when the subnivean space was still well developed and snow depth was still sufficient to allow animals free egress and ingress over the pen wall. Although some temporally extensive supranivean movements outside of the pen did occur, the experimental animal always returned to its burrow inside the pen. The third and fourth experimental runs were carried out on the same individual several weeks later. Snow depth had decreased to the point where the wall was once again a barrier, and the subnivean space had begun to collapse. In the interim period, wild voles that had earlier gained access to the pen from outside were removed by extensive live-trapping, and the experimental animal was effectively isolated. Distances travelled during the latter two runs exceeded those from the earlier two. This apparent increase could be a response to increased food demands for spring weight gain (Dyke, 1971; Sealander, 1972), to decreased food accessibility due to collapse of the subnivean space, to a changing hormonal balance in relation to increasing day-length, or to any combination of these factors. In any case, one or several of these factors could provide sufficient stimulus for spring dispersal even in the absence of social factors such as intraspecific aggression.

Energetics

Great care must be exercised when attempting to affix absolute energetic values to each component of an activity pattern. If the attempt is made in a laboratory situation which is homogeneous and highly artificial, measurements of energy consumption may be technically accurate but misleading because of behavioral modifications caused by the set-up, especially for activity outside the nest (Grodzinski and Gorecki, 1967; Ashby, 1971). Therefore, in order to reduce this error, it is desirable to create an experimental situation in which an animal behaves as naturally as possible. When this is accomplished, accurate measurements of energy consumption can be made during all phases of activity, and information from the present study may then be used to calculate the energetic cost of each component of activity in relation to season and reproductive conditions.

SUMMARY

1. The period and duration of the short term (2-5 hr.) activity rhythm remained relatively constant on a 24 hr. basis throughout the year, and changed significantly only in lactating individuals. The rhythm appears to comprise both endogenous and feeding components.
2. Voles exhibited a strong nocturnal circadian rhythm in summer, apparently entrained by sunrise and sunset, and a more weakly entrained diurnal rhythm in winter.
3. Temporary shelters were apparently used during feeding, and probably played an important role in protecting animals from

predation and environmental stress.

4. Rather than changing the frequency or duration of their activity periods, animals adjusted their exposure time to the seasonally changing external environment by varying the intensity of use of temporary shelters and to a limited extent the amount of extra-nest activity. However, there was no evidence of food storage in home burrows.

5. There appeared to be greater seasonal preferences for home burrows than for temporary shelters, and individual home burrows were frequently used by several experimental voles in quick succession. There was also evidence of burrow sharing with wild voles and deer mice during winter when deep snow allowed them to enter the pen.

6. Significant increases in diurnal activity and movements of lactating individuals likely reflected a substantial increase in their energy requirements over those of other individuals in the same season.

7. Movements among anestrous animals were most localized in early winter before the snow cover was stabilized, and most extensive in late winter and early spring during snowmelt. This extensive movement in the absence of other individuals suggests that a stimulus for spring dispersal may exist in the absence of intraspecific aggression.

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